THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SECOND SERIES.]

No. 114. JUNE 1857.

XXXIII.—*Researches on the Development of the Pectinibranchiata.* By J. Koren and D. C. Danielssen.

[Concluded from p. 366.]

Purpura lapillus (*Buccinum*), Linn.

The capsules in which the eggs are enclosed somewhat resemble a little bottle, of which the convex bottom would be turned upwards, and the very slender neck directed downwards. It is by the lower extremity that they are fixed either to stones or other bodies. Each capsule is hermetically closed, and filled with a viscous fluid, as transparent as water, and resembling white of egg, containing a multitude of eggs (from 500 to 600 or even more). The eggs are of a globular form, furnished with a delicate chorion, a vitelline membrane, and a vitellus consisting of a fluid containing small granules. Amongst the smallest of these granules there are, as in *Buccinum*, a quantity which are oval, and refract light very strongly. We could not distinguish either a germinal vesicle or a germinal spot. After an interval of several days, a commencement of segmentation appeared in the eggs, which divided first into 2 and then into 4 spheres of segmentation. These stages passed pretty regularly. But then a great irregularity made its appearance in the segmentation: we soon saw some of the spheres divide, while the others remained intact; in others, 4 small spheres were formed between the 4 large ones; and others, again, had become divided into 12 or 18 irregular spheres. It was not rare to find eggs which had not yet undergone segmentation; some were also found in which the segmentation had progressed a little way, and in which the chorion was not yet ruptured. In our first memoir* we have given figures of these eggs, and new observations have proved their correctness. In this way we observed a number of eggs, which,

* This memoir will be found translated in the Scientific Memoirs, new series, Nat. Hist. division, p. 330, plates 10, 11 & 12.

although deposited at the same time and enclosed in the same capsule, nevertheless exhibited a great diversity in the progress of their segmentation. We did not observe any nucleus in the spheres of segmentation. Nordmann did not detect them in *Tergipes*, *Rissoa*, and *Littorina*. We have had the opportunity of observing the little clear body which Dr. Carpenter has seen quitting the egg, and which we had not previously noticed. Some days later in the development, the viscous liquid, which filled the capsules, began to grow more fluid, so that the eggs could be made to escape with the greatest ease; they were then conglomerated, and apparently formed a compact mass. On examining this more closely it was found to consist of several adherent groups, which were of different sizes, although they had no distinct forms. Under the microscope, these groups proved to consist of eggs, placed one upon the other like a mass of balls, of which the greater number were in different stages of segmentation, whilst others were not. On the sixteenth day the groups had usually become more distinct, more clearly circumscribed, and more detached from the common mass; they had acquired a cylindrical or pyriform shape. Each of these groups was formed by the union of eggs imbedded in a glutinous mass and covered by a delicate membrane, which was soon furnished with very fine cilia. The eggs themselves had undergone no subsequent segmentation, as the act of progressive segmentation had stopped as soon as the conglomeration was effected. At the side of the upper part where the embryos were attached to the common mass, we could detect an exuded, greyish, semitransparent, and finely granular mass, which had the appearance of increasing the membrane, the outer margins of which began to be furnished with some cirrhi. Whilst the membrane was increasing more and more at the point just mentioned, a similar, yellowish, exuded mass was perceived nearly at its middle; this forms the base of the future foot (Pl. XVII. fig. 3 *d*). The embryo thus formed began to move a little by the aid of its cilia and of some cirrhi; it was in fact observed to make feeble efforts in different directions, as if seeking to detach itself from the common mass; and when at length, after various futile attempts, it succeeded in doing this, it began immediately to turn upon itself. We have seen all the individuals, one after the other, detach themselves and move off in this way, until all the groups had become developed into embryos. We may believe that in this animal, as in *Buccinum*, the number of eggs which combine to form the future embryo is perfectly fortuitous; for not only can we discover no rule for this formation, but, moreover, we find that these aggregates are formed of very different numbers of eggs. Thus, in the same capsule we have seen embryos produced by the union of 3–4 eggs, whilst 60 or more have cooperated in the formation of the majority of the individuals. The difference in the size of the individuals also depended upon the same cause. Their size varied considerably, and embryos of $\frac{1}{4}$ to 1 millim. were seen moving in the liquid then contained in the capsule. As the size of the embryos was variable, so was their number. This depended on the greater or less number of eggs which had cooperated in the formation of each individual. We have found, on the average, from 20 to 40, rarely more.

After the formation of the ciliary membrane, the organs of motion and the foot are the parts which first make their appearance. Nearly at the same time we see between the membrane and the conglomerated eggs a transparent and finely granular mass. In this are developed cells, which unite in layers with the above-mentioned membrane, and give origin to the mantle. The lowest part of the latter secretes a tolerably clear and glutinous liquid, which increases gradually, and forms the rudiments of the shell; this at its first appearance resembles a perfectly clear and gelatinous membrane, in which calcareous particles are afterwards deposited. These gradually become compact, and in this way render the subsequent investigations difficult. The rotatory organs are small at their first appearance, but their volume increases by degrees, so that they acquire more and more the form of a funnel. A multitude of cilia appear on their surface, and cirrhi make their appearance at their superior margin, and cause far more lively movements. In the foot, which is now clearly detached from the rotatory organs and has acquired a nearly square form, a mass of cells furnished with a nucleus makes its appearance. The margins are almost always inclined towards the ventral part of the animal, giving it a striking resemblance to a hollow cylinder; and as all its surface and its margins are furnished with cilia, the whole acquires the appearance of a ciliated canal. It increases rapidly in volume, and exhibits at its base the first rudiments of the auditory organs, which are formed as in *Buccinum*. At the same time we also observe the two pyriform salivary glands, which are placed close to the foot, of a yellowish colour, and filled with a quantity of round cells and pigment-grains. When the development has advanced a little further, the tentacles appear in the form of two conical eminences, at the base of which the eyes are discovered in the form of rounded vesicles, filled with a liquid as clear as water, in which some obscure pigment-grains are found. We could not discover any lens in this stage of development.

On the twenty-third day we discovered the heart. It is formed in an analogous manner to that of *Buccinum undatum*. It is also placed on the back, a little towards the right. It contracts strongly, giving forty to fifty pulsations in a minute. It is furnished with primary muscular fibres, having the form of longitudinal tubes a little enlarged above. We found neither granules nor cells in these tubes. In this stage of development, the branchial cavity not being sufficiently deep to contain the whole heart, a considerable portion issues from it and passes the margin of the mantle. Subsequently, when the mantle becomes elongated and covers the back of the animal, its margin is directed more outwards, and removes from the body in such a way that the cavity, becoming deeper and more ample, encloses the entire heart. We have not been able to follow the rest of the circulatory system.

It is not until after these organs are formed that we observe the buccal orifice, with the pharynx and œsophagus, at the point where the rotatory organs meet on the back. The proboscis in this stage is exceedingly short, and its walls are pretty thick, so that the œsophagus is detected with difficulty. It is a cylindrical canal, which runs directly to the stomach. From the stomach, which is small and oval, issues a long and slender intestinal canal, which passes to the right, then returns to the opposite side, describing a curve, and at length terminates a little towards the right by an anus projecting into the branchial cavity. The œsophagus and also the stomach and intestines are clothed with cilia on their inner surface.

The salivary glands have also become enlarged; their cells are more approximated, and form long rows. In their broadest part a multitude of yellow pigment-grains are seen. In their more slender portion, which is turned towards the œsophagus, the excretory duct of the gland makes its appearance, and becomes elongated to meet the œsophagus. The salivary glands in the adult animal form a coherent mass, but their double excretory duct clearly indicates that this was formerly divided. On each side of the œsophagus we perceive the two cerebral ganglia, which are here distinguished from the common mass by their yellow colour. These ganglia are united to each other by a commissure, and give origin to two other commissures, which unite them with the two pedal ganglia. We have found it impossible to trace the nervous system any further, all the parts of the body having rapidly become opake. We suppose, however, that it agrees for the most part with that of *Buccinum*. It is also about the period at which the nervous system appears, that we distinguish the first traces of the branchiæ, the siphon, and the retractor muscles of the foot. The branchiæ originate from the margin of the mantle, where they form a hollow cylinder, which is twisted to form loops; cilia are seen on its inner margin. It afterwards becomes a little flattened, at the same time dilating considerably. In its walls we discover longitudinal and transverse fibres, and the cilia of the middle of each loop are of extraordinary length. After the production of the branchiæ it becomes extremely difficult to investigate the formation of the other organs; on the one hand because the animal rarely elongates itself sufficiently out of its shell to allow its parts to be perceived, and, on the other, because the mantle has become a good deal thickened, and the shell has been the seat of a considerable deposit of calcareous matter. This shell has acquired the form of that of a Nautilus. The rotatory organs diminish considerably in size. The foot, which is lobate above, acquires more and more the form of that of the adult animal. The operculum, which serves to close the aperture of the shell, is completely developed. The heart, in this stage, is divided into two chambers. The lenses of the eyes are clearly distinguished: we have pretty frequently found a single eye which presented two projections of pigment, each provided with a lens.

The branchial cavity, of which the inner surface is clothed with cilia, has become, at this period of development, sufficiently deep to contain the heart entirely. The margin of the mantle which is furthest removed from the body of the animal is furnished with cilia, and at the bottom of the branchial cavity we for the first time discover a contractile vesicle (kidney), similar to that which exists in *Buccinum undatum*. After the lapse of eight weeks, the young animals have not yet quitted the capsules, and when one is taken out in this state, it sets itself to creep like the adult animal, with the foot, the tentacles, and the siphon extended. It is then distinguished from the adult in that the rotatory organs have not entirely disappeared, that the shell is not hard, and also by the spire, which has only one, or at most, two turns. During the ninth or tenth week the young animals quit the capsules; the rotatory organs have then disappeared, and behind the tentacles we observe a raised line, which indicates the place previously occupied by them.

The shell has become more elongated, and approaches nearer to that of the adult; it is hard, brittle, and nearly opake, but the last turns of the spire are not yet developed. We have not referred to the way in which the development of the organs takes place, because it does not differ from that which occurs in *Buccinum undatum*. But, before concluding our memoir on the development of the Pectinibranchiata, we find that it is necessary to make a few observations on the memoir of Dr. Carpenter on *Purpura lapillus*, as the results which he has obtained are very different from ours.

We shall indicate the most remarkable features of this memoir in the author's own words: "The general result of my observations is, that the process has been altogether misconceived by my predecessors; that no such departure from the ordinary plan of development takes place as the fusion of a number of originally distinct ova into a single embryo; but that each embryo originates in a single ovum; that it attains to a certain grade of development by the metamorphosis of the contents of its own vitellus; but that its increase in size, and the continuance of its development, depend upon its appropriation, by a process of deglutition or swallowing, of a mass of additional or supplementary vitellus, the want or insufficiency of which occasions its partial or complete abortion. As to the immediate cause of the production of 'monstrous' embryos, therefore—a phænomenon which I have found to be far more common than MM. Koren and Danielssen supposed,—I am in accordance with my predecessors, as I attribute it, with them, to the deficiency of nutritive material. But I differ from them essentially, not merely in regard to the mode in which this nutritive material is appropriated, but also in asserting that the production of embryos from single ova, instead of being an abnormal and occasional phænomenon, is one stage in the normal process of development." The number and volume of the "egg-like bodies," which is the name given by the author to the eggs enclosed in the capsules, agree with our observations upon these eggs. But he was unable to discover the chorion, which, however, appeared to us to be very distinct, and which could sometimes be seen even after the commencement of segmentation. He did not observe either a germinal vesicle or a germinal spot in these "egg-like bodies," but on causing nearly developed eggs to escape from the ovaries, he found that they were of the same volume as the "egg-like bodies," and furnished with a germinal vesicle and germinal spot. We agree perfectly with this.

However, Dr. Carpenter states that, independently of the "egg-like bodies," he has found true eggs in each capsule. But, on asking himself what difference there was between these true eggs and the "egg-like bodies," he has only been able to find a very slight variation in their segmentation. He says that the first segments of the vitellus of these true eggs divide into several small parts, and that by this means a clearer peripheric layer is formed, which becomes enveloped in a ciliary membrane, whilst the "egg-like bodies," which are the largest, have not yet undergone segmentation. He also adds, that segmentation certainly takes place in the "egg-like bodies," but that it is not so complete, and appears to be more fractional, and intended to divide each "body" into smaller spheres. Dr. Carpenter also asserts that from these eggs an embryo is developed, which swallows as many as it can of the "egg-like bodies," and that, being thus furnished with materials, it proceeds in its development. When the embryo cannot catch the crushed "egg-like bodies," it dies from want of nourishment.

It is easy to see that Dr. Carpenter has fallen into an error, and it is to be regretted that he should have allowed himself to be misled by a prejudice, as owing to this his observations have become obscure and confused. It is incomprehensible how he could imagine that he could distinguish the true eggs from the "egg-like bodies" only by the difference which he professes to find in their segmentation, as he ought also to know that the segmentation is sometimes very different even in animals of the same species; and he states that the segmentation in *Purpura lapillus* is very irregular. The segmentation, however, is his sole point of support, for he himself says that, with the exception of this, the eggs enclosed in the capsules (even his "egg-like bodies," as well as his true eggs) are anatomically and physiologically alike. In one word, he could find no perceptible difference.

In this we agree with Dr. Carpenter. In our memoirs we have proved that all the bodies which are enclosed in the capsules have a chorion and a vitelline membrane, and that their segmentation is not arrested by the commencement of the act of conglomeration. We have shown that all these eggs may be included in this act, but that in each capsule there are usually one or several eggs which become developed before the act of conglomeration has commenced, and that the embryos which are developed by these isolated eggs die very soon from the deficiency of material necessary for the formation of the organs. It is these embryos developed from a single egg which have led Dr. Carpenter astray: he has seen a plank of safety for his ideas of unity, and it is for this reason that he has made his creatures devour everything which might alter the law which he believes to be the foundation of all development. Thus, as soon as the embryos previously mentioned were formed, they would proceed to unite themselves with the conglomerated eggs to seek their nourishment: for this reason they would be furnished with a mouth and an œsophagus. Dr. Carpenter has given us the figure of such a mouth and œsophagus, both beset with cilia; and then, by the agency of this mouth they would attach themselves to the conglomerate. Here, however, is his greatest error; for what he gives us as the mouth and œsophagus is the foot in its different stages of development.

This occurs in the following way. The foot, in its first development, projects and slightly passes the rest of the common mass, and acquires a rolled-up form, for its margins are curved inwards towards the plane. When we examine it superficially in this state, we find that it has some resemblance to a canal. But on observing it attentively, we soon recover the right road. In following the development of the foot, we see changes of form and structure, as well as the auditory organs at its base. If the English physiologist had done this, he would have been convinced that at first there was no mouth or œsophagus, and that therefore there could be no question of devouring the conglomerated eggs. But he would also have been able to ascertain that a group of eggs in different stages of segmentation is surrounded by a membrane, and that organization commences subsequently. It is curious, however, that Dr. Carpenter did not inquire what became of the foot of his embryos, as he is perfectly aware that this organ makes its appearance very early in the Mollusca, while he only speaks of the foot when it is completely developed, both as regards form and structure. But he observed a mouth and œsophagus, and full of the idea of the formation of these organs, he completely forgot the foot, which, however, is of considerable importance in the Mollusca..

In spite of all this, Dr. Carpenter would perhaps have avoided these errors if he had employed an intense light from above, for he would then have seen how the eggs in different states of segmentation were placed in layers, like a heap of balls, in the interior of the membrane, of which we have already spoken sufficiently (Pl. XVII. fig. 2). If he had crushed an embryo of this kind, he would also have been convinced that the entire eggs were placed one upon the other, as they occur in the conglomerate before the envelopes of the embryos are formed. With an ordinary light, he would have observed in a mass of embryos, towards the inner surface of the membrane, entire eggs, which allowed their spheres of segmentation to be seen distinctly. But this could not be the case if Dr. Carpenter was right, as he does not believe that these little creatures swallowed entire eggs; this, however, has also escaped him. When he states that he has seen how the embryos eat and swallow the vitelline mass, this is an illusion, for it sometimes happens that some vitelline segments attach themselves to the foot itself, long after the embryo has detached itself from the conglomerate; but, far from swallowing them, it endeavours with all its power to get rid of them, in which it most frequently succeeds.

Dr. Carpenter also indicates that we have deceived ourselves with regard to the development of the heart, and states that we have taken the contractile vesicle (kidney) for the heart. He asserts that the latter is not formed until after the contractile vesicle, and that it occurs deeper in the branchial cavity. This is also an error on the part of Dr. Carpenter; it is himself, again, that is deceived; and we can affirm this without fear, as by our frequently-repeated observations we have confirmed our first impressions. And when, in conclusion, Dr. Carpenter asserts that we have also made several mistakes in the ulterior development, we are led to believe, from all that we have just explained, that Dr. Carpenter has no right to reproach us therewith. But before concluding these remarks, we should state that our observations on *Buccinum undatum* and *Purpura lapillus* no longer stand alone; for, without taking into account that M. Leuckart has made different observations equivalent to ours in the article "Zeugung," in 'Wagner's Handwörterbuch der Physiologie,' M. Lindström has shown, in the 'Öfversigt af Konglige Vetenskabs-Akademiens Förhandlingar 1855,' that the embryo of *Neritina fluviatilis*, Linn., is developed in a similar manner to that of *Buccinum undatum* and *Purpura lapillus*. The egg-capsules contain 30–40 eggs, from which only a single individual is developed.

EXPLANATION OF PLATES XVI. AND XVII.

[The figures here given are only a selection from those of the authors.]

Plate XVI. Magnified about 150 diameters.

Fig. 1. Grouped eggs and newly-formed embryos of *Buccinum undatum*, the greater part of which are already furnished with rotatory organs, foot, auditory organs, salivary glands, and heart: *a*, the mass exuded from the eggs; *b*, the softened chorion; *c* & *d*, membrane surrounding the eggs; *e*, an embryo formed by a single egg.

Fig. 2. An embryo seen from the ventral surface: *a*, membranous shell; *b*, mantle; *c*, eggs; *d*, heart; *e*, rotatory organs; *f*, foot; *g*, auditory organs; *h*, salivary glands; *i*, pharynx; *k*, œsophagus; *l*, stomach; *m*, branchiæ.

Fig. 3. An embryo seen from the side: *a*, shell; *b*, eggs; *c*, foot; *d*, rotatory organs; *e*, tentacles with eyes; *f*, heart; *g*, the large cerebral ganglia; *h*, the small cerebral ganglia; *i*, commissures of the pedal ganglia; *k*, auditory organs; *l*, commissures of the branchial ganglion; *m*, branchial ganglion; *n*, nerves of the intestines; *o*, pedal ganglia; *p*, salivary gland; *q*, branchia; *r*, retractor muscle; *s*, stomach; *t*, intestine; *u*, liver, and above this the contractile vesicle (kidney).

Fig. 4. An embryo seen from the side: *a*, shell; *b*, siphon; *c*, foot; *d*, operculum; *e*, tentacles.

Plate XVII.

Fig. 1. Nervous system of an embryo, somewhat compressed, magnified about 200 diameters: *a*, the two large cerebral ganglia; *b*, the two small cerebral ganglia; *c*, the two large pedal ganglia;

d, branchial ganglion; *e*, intestinal ganglion; *f*, the two small pedal ganglia; *g*, commissures of the small cerebral ganglia to the pedal ganglia; *h*, commissures of the large cerebral ganglia to the branchial ganglion; *i*, commissures of the large pedal ganglia to the branchial ganglion; *k*, auditory nerves; *l*, optic nerves; *m*, nerves (commissures) of the large pedal ganglia to the small pedal ganglia; *n*, nerves which arise from the large pedal ganglia, and ramify; *o*, nerves of the small pedal ganglia, which also ramify; *p*, nerve of the intestinal ganglion; *q*, nerve of the heart; *r*, nerves of the intestines.

Magnified about 150 diameters.

Fig. 2. An embryo of *Purpura lapillus* recently detached from the common mass of eggs: *a*, conglomerated eggs; *b*, membrane furnished with cilia; *c*, the commencement of the rotatory organs, furnished with cirrhi.
Fig. 3. An embryo seen from the back: *a*, *b*, *c*, as in the preceding figure; *d*, the foot further developed and furnished with cilia.
Fig. 4. An embryo seen from the back: *a*, *c* & *d*, as in the preceding; *b*, the shell; *e*, salivary glands; *f*, tentacles; *g*, eyes; *h*, heart; *i*, mantle.

The following Figures are magnified about 200 *diameters.*

Fig. 5. An egg of *Buccinum undatum* in which the vitellus has divided into numerous spheres of segmentation: *a*, membrane; *b*, spheres of segmentation.
Fig. 6. An embryo formed by a single egg, of which the vitellus has divided into two spheres of segmentation: *a*, exuded mass; *b*, two spheres of segmentation.
Fig. 7. An embryo also formed by a single egg, in which some organs are already formed: *a*, membranous shell; *b*, mantle; *c*, two spheres of segmentation; *d*, rotatory organs; *e*, foot.
Fig. 8. The embryo of one egg, seen from the ventral surface, and in the centre of which four spheres of segmentation are seen: *a*, membranous shell; *b*, mantle; *c*, four spheres of segmentation; *d*, rotatory organ; *e*, foot, with auditory organs.
Fig. 9. An embryo with eight equal spheres of segmentation: *a*, membrane; *b*, spheres of segmentation.
Fig. 10. The same embryo a little more advanced in development.
Figs. 11, 12. The same embryo, more advanced: *a*, shell; *b*, mantle; *c*, spheres of segmentation; *d*, rotatory organs; *e*, foot.
Fig. 13. An embryo seen from the ventral surface: *a*, membranous shell; *b*, mantle; *c*, spheres of segmentation; *d*, rotatory organs; *e*, salivary glands; *f*, œsophagus; *g*, pharynx.
Fig. 14. An embryo seen from the back: *a*, *b*, as in fig. 13; *c*, rotatory organs; *d*, foot; *e*, salivary glands; *f*, stomach; *g*, pharynx.
Fig. 15. An embryo formed of three eggs, seen from the back: *a*, *b*, as in fig. 13; *c*, vitelline mass; *d*, *e*, as in fig. 13; *f*, foot; *g*, pharynx.
Fig. 16. An embryo seen from the back: *a*—*f*, as in preceding; *g*, stomach; *h*, œsophagus.
Fig. 17. An embryo formed by three eggs: *a*—*g*, as in fig. 16; *h*, pharynx; *i*, heart.